Modeling regional-scale habitat of forest birds when land management guidelines are needed but information is limited

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ABSTRACT

Conservation planning at broad spatial scales facilitates coherence between local land management and objectives set at the state or provincial level. Habitat suitability models are commonly used to identify key areas for conservation planning. The challenge is that habitat suitability models are data hungry, which limits their applicability to species for which detailed information exists, but managers need to address the needs of all at-risk species. We propose a modeling approach useful for regional-scale conservation planning that accommodates limited species knowledge, and identifies what managers should aim for at the local scale. For twenty at-risk bird species, we built models to identify potential habitat using both literature information and empirical data. Species occupancy within potential habitat depends on the presence of intrinsic elements, which we identified for each species so that managers can enhance these elements as appropriate. For most species, the estimated amount of habitat needed to meet population targets was <10% of the mapped potential habitat, with notable exceptions for Northern Goshawk (*Accipiter gentilis*; 100%), Brown Thrasher (*Toxostoma rufum*; 63.7%), and Veery (*Catharus fuscescens*; 17.9%). Model validation showed that interior forest species models performed best. Our modeling framework allowed us to build potential habitat models to various endpoints for different species, depending on the information available, and revealed a number of species for which basic natural history data are missing. Our potential habitat models provide regional perspective and guide local habitat management, and assist in identifying research priorities.

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1. Introduction

Conservation is most effective when conducted on a broad spatial scale (Noss, 1983) because this scale allows consideration of the ecological context within which habitat occurs (Margules and Pressey, 2000). Conservation planning at broad spatial scales (e.g., region-wide, or state/province-wide) facilitates coherence between land management actions at the local scale and objectives set at the state or provincial level. However, to be adopted by land managers and translated into on-the-ground action, regional-scale conservation planning must answer specific questions: how much habitat is available, how much is needed, and where should it be protected, enhanced, or restored?

Regional-scale conservation planning has been used to evaluate patterns and processes such as landscape connectivity (Rouget et al., 2006; Levin et al., 2007), human-caused threats (Woolmer et al., 2008), sometimes integrating species-specific habitat requirements (e.g., Pearce et al., 2008). However, conservation planners have thus far been restricted in their ability to simultaneously (1) contend with species for which we have limited knowledge and (2) identify concrete actions needed at the local scale within a regional perspective.

Knowledge of a species' habitat requirements is necessary for management interventions, and habitat models are commonly employed to identify conservation actions.

One class of habitat models which use inductive reasoning generalizes habitat relationships based on a sample of observations (Ottaviani et al., 2004); this class includes habitat selection models (e.g., resource selection functions; Johnson et al., 2004) and habitat distribution models (e.g., niche-based models; Brito et al., 2009). Inductive models, which are used to explain wildlife distribution and predict occurrence, have limitations when used at the regional scale. First, there are limits to applying habitat models at a regional scale when they were built from data gathered at a finer scale. Habitat relationships identified in a relatively small study area

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may be the result of local availabilities and adaptations, limiting extrapolation outside of the study area (Railsback et al., 2003; Early et al., 2008). Second, habitat models derived from long-term field surveys are rare (e.g., 5–6 years of surveys; Mitchell et al., 2006). In shorter-term studies, fluctuations in population size, population cycles, or metapopulation dynamics can lead to habitat models built from an unrepresentative snapshot of the population (Hobbs and Hanley, 1990; Heglund, 2001). A statistical, inductive habitat model can successfully predict a virtual species' habitat when the habitat is fully occupied, but the model may perform relatively poorly when the species occupies only a portion of available habitat and is spreading into unoccupied habitat (Hirzel et al., 2001).

The lack of regional and long-term data can limit the appropriateness of inductive models, and argues for deductive habitat models that integrate information from published literature or expert opinion (Ottaviani et al., 2004). For example, a habitat suitability index model (HSI) can be applied at landscape scales (e.g., Dijak and Rittenhouse, 2009). However, the use of HSI models at regional scales also has limitations: determining appropriate suitability functions is difficult over broad areas (Roloff and Kernohan, 1999), HSI models are sensitive to the choice of land cover data used (Manton et al., 2005), and HSI models can be poor predictors of a species' occurrence (Holmes et al., 2007), especially for habitat generalists (Dettmers et al., 2002). Finally, many HSI models are based on small-scale, local habitat characteristics that are difficult to quantify over large areas. For example the US Fish and Wildlife Service's habitat suitability index (HSI) model for Brown Thrasher (*Toxostoma rufum*; Cade, 1986) is based on variables including woody stem density and litter depth. Currently no method exists to obtain regional-scale coverage for these variables.

Perhaps the most important shortcoming of current habitat models, regardless of the type, is that for many species our knowledge or available data sets are so limited that the development of either inductive or deductive habitat models is difficult. In a context where habitat models are needed for a large number of species, as is often the case when developing management plans for public lands, available modeling approaches are data hungry and not flexible enough to accommodate lesser-known species. There is a clear need for a modeling approach that can incorporate what is known for all species of conservation concern, not just for the best-studied species. Such a habitat model framework would provide the regional perspective necessary to identify management actions needed from the regional level to local management units.

As a strategic approach to encourage regional conservation planning, the US Congress mandated development of a Wildlife Action Plan by each US state and territory. In Wisconsin, the State Wildlife Action Plan identified 152 vertebrate Species of Greatest Conservation Need (SGCN), with the goal of conserving these species and their habitat before they become rare and warrant more costly protection (Wisconsin Department of Natural Resources [WIDNR], 2005). Such a comprehensive selection of conservation targets, sometimes expressed as a goal of "keeping common species common" (Harrison, 2005), is an approach with geographically wide appeal, but new modeling approaches are necessary to meet this goal.

The overarching goal of our study was to evaluate northern Wisconsin's potential to maintain breeding populations of the forest-breeding avian SGCN identified in Wisconsin's Wildlife Action Plan. The first objective of this study was to develop informative habitat models that are appropriate for a regional scale and can accommodate species for which variable amounts of information
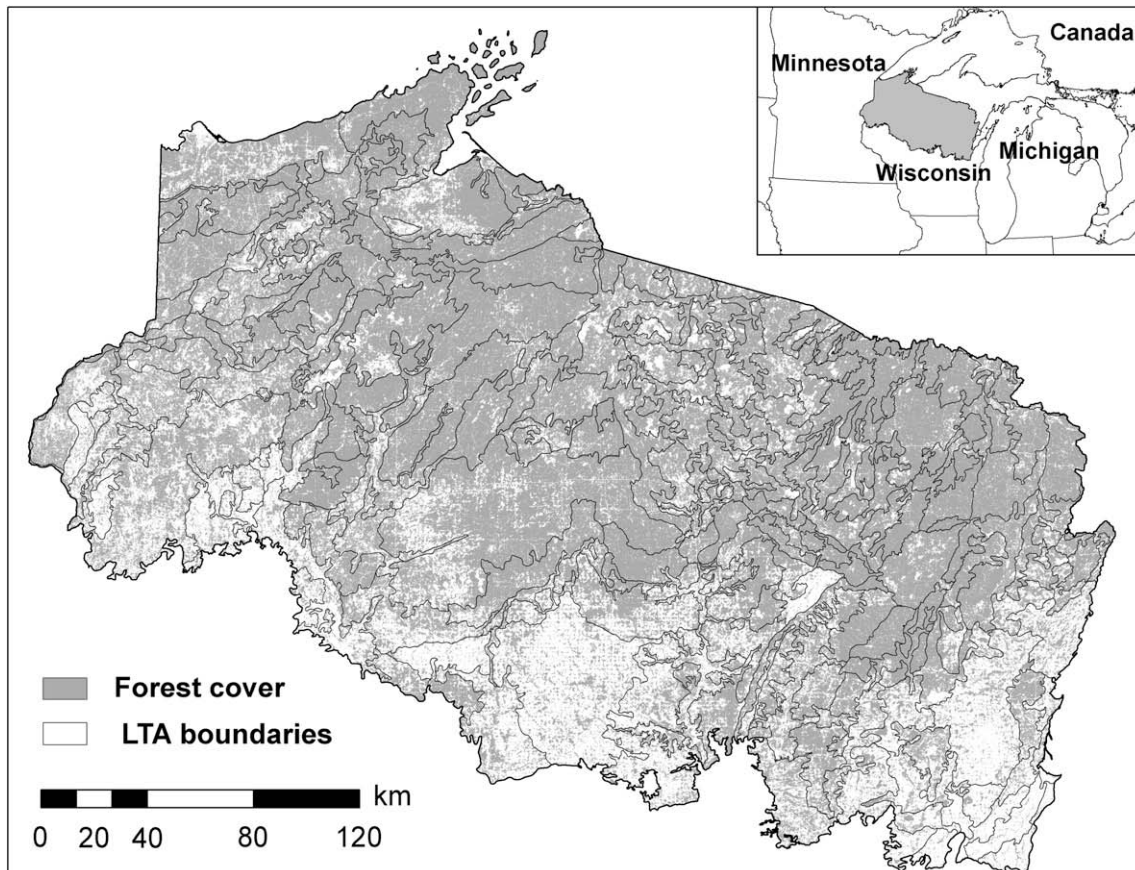

Fig. 1. Study area: northern Wisconsin Laurentian Mixed Forest Ecoregion (Bailey, 1995).

are available. The second objective was to estimate the amount and distribution of potential habitat and the habitat capacity for forest-dwelling avian SGCN.

2. Methods

2.1. Study area

The study area covered most of northern Wisconsin (USA), part of the Laurentian Mixed Forest Ecoregion (Bailey, 1995; Fig. 1). This landscape encompasses 7 million ha, 4.6 million of which were classified as forest in the 2001 National Land Cover Database (NLCD). Extensively logged in the first half of the 20th century, this region has since largely reverted to forests that have re-grown on former clear-cuts and abandoned fields (Radeloff et al., 2005). During this study, common land uses included forestry, recreation, small private woodlots, and agriculture on the best soils. A large fraction of the study area (28%) was publicly owned. Since the 1950s, second-home building has flourished, with development concentrated along lakeshores resulting in significant forest fragmentation (Radeloff et al., 2005).

Temperate forests often receive less conservation attention than other threatened ecosystem types such as grasslands or wetlands, partly because temperate forests are not as rare, but habitat loss and degradation continue to threaten temperate forests. The threats in northern Wisconsin are representative of those elsewhere in northern temperate forests: a lack of large patches and old forests, fragmentation, invasive plant species, overabundant browser populations (e.g., white-tailed deer), loss of specialized ground flora, invasive earthworms, and motorized recreation (WDNR, 2005).

2.2. Study species

Of the 84 avian SGCN in Wisconsin, 20 regularly breed in northern forests (listed in Table 1). We built habitat models for these 20 species, five of which are year-long residents, and fifteen of which are migratory, including thirteen neotropical migrants. The selection of SGCN was based on a species' rarity within the state, its state and global population trends, its global relative abundance and distribution, and the importance of the threats affecting it (WDNR, 2005). The resulting selection is a series of species for which there are varying degrees of conservation concern, from common species with a negative long-term trend (e.g., brown thrasher) to range-restricted, rare and rapidly declining species (e.g., the golden-winged warbler). The need to manage for species reflecting this broad a range of conservation concerns is likely mirrored in many regions of the world.

2.3. Habitat models

Breeding bird habitat relationships are relatively well known for North America, and we obtained general habitat requirements of forest-breeding, northern Wisconsin avian SGCN from published

Table 1
Components included in the potential habitat models for twenty avian forest species of greatest conservation need in northern Wisconsin.

	Habitat group[a]					Constraints[b]	Intrinsic elements[c]
	D	C	M	S	W		
Black-backed Woodpecker		x			x	Coniferous woody wetlands, exclude red pine, 30-ha minimum patch size	Large, deteriorated snags, post-fire or disease dynamics
Black-billed Cuckoo	x		x	x	x	Forest edges (43-m), shores (43-m) of lakes, rivers, and emergent wetlands	Unknown
Black-throated Blue Warbler	x		x			Northern hardwoods, core forest (85-m edge), 500-ha minimum patch size,<13 deer/km^2	Well-developed understory vegetation
Blue-winged Warbler	x			x		None	Dense saplings; early successional or abandoned field
Boreal Chickadee		x			x	Exclude red pine, pine barren, and white spruce forests, only LTAs with relative density of black spruce and balsam fir >12% (from FIA data), coniferous woody wetlands, 5-ha minimum patch size	None
Brown Thrasher	x	x		x		Deciduous edge (43-m), pine barrens, 2.6-ha minimum patch size	Unknown
Canada Warbler		x	x		x	Exclude red and jack pine, core forest (43-m edge removed), coniferous woody wetland, habitat must be within 400-ha minimum forested area	Well-developed understory, ground layer
Cerulean Warbler	x				x	16-ha Minimum patch size	High, closed canopy
Connecticut Warbler		x			x	Pine barrens, coniferous woody wetlands	Dense shrub and herb layers
Golden-winged Warbler	x			x	x	Shrubby wetlands, deciduous forests in LTAs with relative density of aspen >6% (dbh ⩾ 1"; from FIA data)	High herbaceous cover, early successional or abandoned field
Least Flycatcher	x		x			Core (85-m edges removed)	None
Northern Goshawk	x	x	x		x	Deciduous forested wetlands, 2685-ha minimum patch size with ⩾75% habitat	Large canopy trees, sufficient prey base
Olive-sided Flycatcher		x			x	Red pine excluded, coniferous forested wetlands, 15-ha minimum patch size	Snags, tall trees
Red-shouldered Hawk	x		x			Deciduous forested wetlands, within 540 m of emergent wetland, lake or river; 154-ha minimum patch size with ⩾75% habitat	large canopy trees, low ground cover
Red Crossbill		x				None	Mature stands with large cone crop
Spruce Grouse		x			x	Coniferous forested wetlands, exclude red pine and white spruce forests, exclude pine barrens	Early successional, high stem density
Veery	x		x			Core forest (85-m edge removed), 100-ha minimum patch size	Shrubby understory, earlier succession, moist sites
Whip-poor-will	x	x	x			Core forest (43-m edge removed)	Open understory, dry site, adjacent to open habitat
Wood Thrush	x		x			Core forest (43-m edge removed), 1-ha minimum patch size, housing density <20 housing units/square mile (2.6 km^2).	Mature canopy, open understory
Yellow-billed Cuckoo	x		x		x	Forest edges (43-m), shores (43-m) of lakes, rivers, and emergent wetlands	Unknown

[a] Habitat groups represent the coarsest habitat associations for each species; D = deciduous forest, C = conifer forest, M = mixed forest, S = upland scrub/shrub, W = woody wetland. References for the literature used in model building are available as an Appendix in the Supplementary material.

[b] Constraints reflect conditions on the use of habitat groups by species.

[c] Intrinsic elements are important habitat elements, at a finer spatial scale, that cannot be mapped for the extent of the study area.
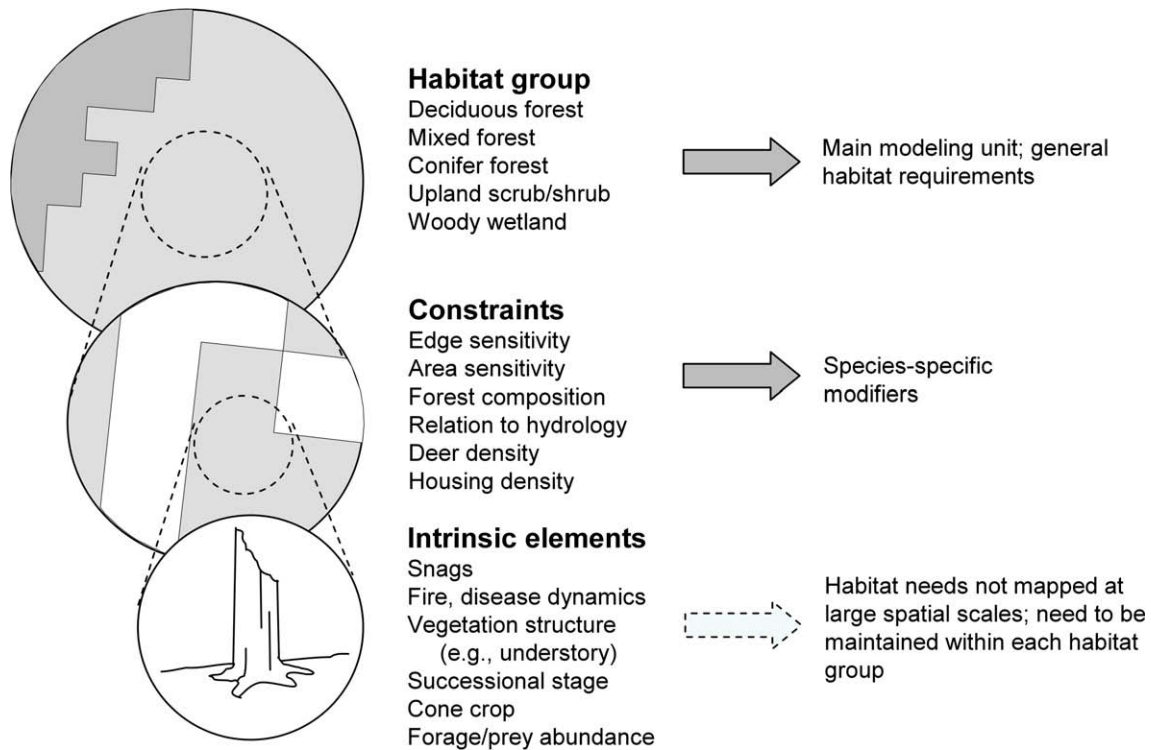
Fig. 2. Nested habitat components considered when building a potential habitat model.

studies, breeding bird atlases, and species accounts. Of the 84 avian SGCN in Wisconsin, 20 regularly breed in northern forests (Table 1). Our modeling approach consisted of three nested habitat components that reflect levels of specificity, category resolution, and data availability (Fig. 2):

> *Habitat groups* are our main modeling unit. These are broad vegetation cover types (e.g., deciduous, mixed, or coniferous forest) that capture the general habitat requirements for a given species. A species may rely on more than one habitat group. Habitat groups' distributions are well mapped at the regional scale.
> *Constraints* are species-specific modifiers to the habitat groups. They refine habitat requirements by taking into account the more specific conditions needed by birds (e.g., edge-sensitivity, exclusion of some stand types, and proximity to water). Constraints allow us to refine the habitat models using parameters that are mapped at broad spatial scales.
> *Intrinsic elements* are fine scale habitat selection requirements. These elements are not usually mapped at the regional scale, but most can be maintained within habitat groups under appropriate management (e.g., snags, understory vegetation).

We combined habitat groups and habitat constraints into habitat distribution models that identified potential habitat. Potential habitat can support species of conservation concern if land management provides the intrinsic elements. Full occupancy of the resulting mapped potential habitat can not be expected, as our model structure accommodates distributions that vary due to environmental conditions or metapopulation dynamics.

2.4. Model building

We developed potential habitat models based on a 30-m resolution regular grid. The first step was to associate each species with one or more habitat groups, which corresponded to the classes of

the 2001 NLCD (Multi-Resolution Land Characteristics Consortium [MRLC], http://www.epa.gov/mrlc/nlcd-2001.html), and to map all areas with the identified vegetation cover. The overall accuracy assessment for the region including the study area was 91.2% (MRLC), but no formal accuracy assessment by category has been done for our region. In another forest region part of the same Ecoregion, accuracy assessments varied from 93–99% for forest categories, 73–100% for wetlands, and 75–82% for scrub/shrub and forested wetland categories (Maine Department of Environmental Protection: http://www.maine.gov/dep/gis/training/melcd/nlcd_2001_landcover_aa_matrix.pdf). We then extracted areas satisfying the habitat constraints that we had identified in the literature. Depending on the species, constraints could include area sensitivity and edge effects, modeled using morphological image processing applied to the 2001 NLCD image classification (Vogt et al., 2007). For some species we used tree species composition to extract tree species from the broader habitat groups. Tree species composition was obtained from the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND, http://www.sco.wisc.edu/wiscland). We only used WISCLAND classes for which accuracy was assessed as greater than 75% with >450 verification sites (WISCLAND User Guide, http://dnr.wi.gov/maps/gis/datalandcover.html). When needed, tree species composition and diameter classes were integrated using the US Forest Service Forest Inventory Analysis data (FIA; Miles et al., 2001) from the 5th cycle (1996), summarized by land type association (LTA). LTAs are the finest level of the National Hierarchical Framework of Ecological Units, and delineate areas that share characteristics such as landform, topography, hydrology, soils and potential natural vegetation (Avers et al., 1994; Fig. 1). The study area consisted of 150 LTAs, with a median size of 29 132 ha (range: 2118–385 000 ha). When a composition or diameter class threshold was met within a LTA polygon, it was used in the model – otherwise it was not used. For bird species affected by high deer density (and the resulting reduced understory vegetation), we used

a maximum threshold of winter deer density, based on the 2007 population estimate of the WIDNR. We used deer management units in the same way we used LTA polygons, to delineate areas that were included in the models. We located water bodies using a 1:24 000 hydrology layer developed by the WIDNR, while wetlands were identified from the 2001 NLCD. We used housing density at the partial census block level (partial block group median size in the study area: 163 ha) for the year 2000 as a model variable, for species known to avoid settlements (Radeloff et al., 2005).

Most habitat constraints consisted of a binary choice (e.g., red pine forests were excluded from a model based on the literature), but some constraints took the form of an inclusion threshold (e.g., only areas with an average winter deer density <13 deer/km^2 were included). We established the value of that threshold by training the models using data from the Wisconsin Breeding Bird Atlas, a statewide survey effort conducted from 1995 through 1999 (Cutright et al., 2006). The Atlas reports evidence of breeding for each of the state's 7.5-min USGS topographic quadrangles (approximately 150 km^2). When a threshold value needed to be determined, we adjusted the value iteratively until there was visual agreement between the potential habitat model and the Atlas data.

Intrinsic habitat elements were not used to build potential habitat models, but identifying these unmapped elements can assist in determining management actions that promote occupancy. We identified intrinsic elements from the literature, preferably from studies conducted in the study region, and from a state wide bird conservation plan that synthesizes the requirements and recommendations for all SGCN (Kreitinger and Paulios, 2007).

2.5. Model evaluation

A formal test of the models with empirical data was not possible here, because potential habitat models do not attempt to represent occupied habitat. Nevertheless, to assess the relationship between potential habitat models and actual bird habitat, we evaluated each model for correspondence with data from six studies using standardized 100-m, 10-min circular point-counts (Howe et al., 1997), collected between 1987 and 2005 (Howe and Roberts, 2005; Danz et al., 2007; R.W.H., unpublished data; B.R. Bub, unpublished data), as well as occurrences from the period 1992–2007 recorded in the Wisconsin Natural Heritage Program archive. These data were collected independently from the Wisconsin Breeding Bird Atlas program. Evaluations were conducted at the LTA level, in two ways: first, the proportion of each LTA's area defined as potential habitat was calculated, and compared with the mean number of detections per survey location using Spearman rank correlation, using only the survey locations where the species was detected. This provided an indication of the correlation between the model and the species' abundance. Secondly, we evaluated the potential habitat models' omission error rate at the LTA level, calculated as 1 – (the number of occupied LTAs for which no potential habitat was predicted/the number of occupied LTAs). We chose LTAs as the unit of evaluation for three reasons: (1) the spatial resolution of LTAs is broad enough to accommodate classification errors in the remote sensing data used, (2) LTA size is a reasonable level of detection location specificity given the "coarseness" of the potential habitat models, and (3) land managers in the study area use LTAs as management units.

2.6. Analysis of habitat capacity

We estimated habitat capacity by dividing the total area of potential habitat by the published territory size or by multiplying by density estimates. This capacity estimate assumes all intrinsic elements of a species' habitat requirements are present throughout the mapped potential habitat. We also calculated habitat capacity

estimates with intrinsic elements present in 10% and 50% of the mapped potential habitat since intrinsic elements are unlikely to be present everywhere. The habitat capacity estimates were then compared to state-level population estimates from Partners in Flight (PIF; Rich et al., 2004). These estimates were based on North American Breeding Bird Survey data (BBS; Sauer et al., 2005) adjusted with three modifications (Rich et al., 2004). First estimates were doubled based on the fact that typically only males are detected by song. Second, in order to account for a decreasing detection probability with distance from the BBS route, a detection-area adjustment was made by allocating each species to one of five effective detection distances. Time-of-day variations in detectability were accounted for with a third statistical adjustment. Thogmartin et al. (2006) provide a critical review of this approach. We re-scaled the Wisconsin PIF estimates to the study area by using a grid of abundance based on 1994–2003 BBS data (Sauer et al., 2005) to determine the proportion of the state-level population that occurred within the study area.

We reported, for each species, the proportion of the global population occurring in Wisconsin, the global PIF population objectives, and a PIF conservation priority score for the Boreal Hardwood Transition region (Panjabi et al., 2005). We applied the PIF range-wide population objective to the current population estimate for Wisconsin and estimated the minimum amount of habitat needed, using territory size or density estimates obtained from the literature. When a range of territory sizes or density estimates were available, we chose those from studies within or close to our study area. When estimates from multiple studies close to our study area where available, we selected the value that would lead to the most conservative minimum amount of habitat needed (i.e., the largest mean territory size or smallest density). In the absence of PIF population objectives, we calculated the minimum amount of habitat needed to maintain the PIF population estimate.

3. Results

We built potential habitat models for 20 avian SGCN that breed in forested areas of northern Wisconsin (Table 1, e.g., Fig. 3). Each model integrated 1–4 habitat groups, with deciduous forest being the most common group (13 species). Forest edge was taken into account for nine species, either as a habitat itself (three species), or as an adverse environment excluded from the models (six species). Area sensitivity was included for 11 species, with large minimum patch sizes (⩾400 ha) for three species. For two species (Blue-winged Warbler [*Vermivora pinus*] and Red Crossbill [*Loxia curvirostra*]), we could not identify habitat constraints. For Boreal Chickadee (*Poecile hudsonica*) and Least Flycatcher (*Empidonax minimus*) all the relevant habitat components reported in the literature were captured by the habitat group and constraints alone.

For Black-billed and Yellow-billed Cuckoos (*Coccyzus erythropthalmus* and *Coccyzus americanus*), and Brown Thrasher, no intrinsic elements could be identified for the study region. Overall, the most commonly identified intrinsic elements involved one or more specific seral stage (10 of 20 species) and level of understory development (8 of 20 species; Table 1).

We carried the analysis of potential habitat to various endpoints for different species, depending on the availability of data (Fig. 4). The limitations we identified included incomplete information on habitat requirements, limited ability to detect habitat requirements at large spatial scales, insufficient evaluation data, and unknown territory size or density.

Different levels of concordance were apparent between the training data and the potential habitat models. Some models corresponded well with evidence of breeding (e.g., Canada Warbler
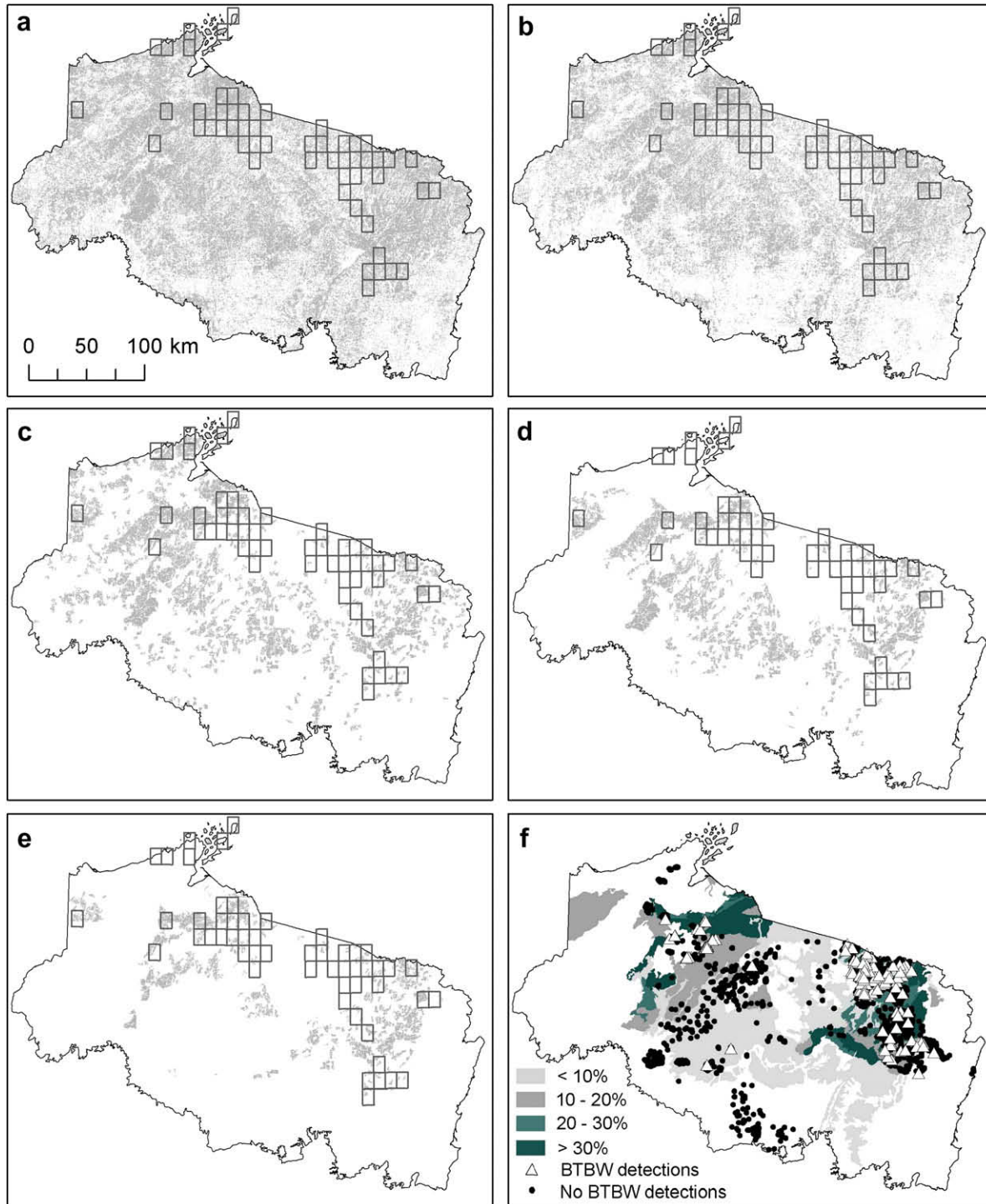
Fig. 3. Potential habitat model development for the Black-throated Blue Warbler. On panels (a)–(e), the progressively constrained potential habitat is shaded gray, and the rectangles represent areas where breeding has been reported. Panels identify (a) habitat group alone (deciduous and mixed forest), (b) core forest only, based on a 85-m edge, (c) patches 500 ha or larger, (d) LTAs with 10% or greater forest composition of northern hardwoods, (e) deer management units with <13 deer/km². The evaluation data are shown in (f), with LTAs highlighted to reflect proportion of the area occupied by potential habitat.

[*Wilsonia canadensis*], Golden-winged Warbler [*Vermivora chrysoptera*], Fig. 5a and c), and others identified extensive potential habitat outside areas where breeding activity was recorded (e.g., Boreal Chickadee, Fig. 5b). For a few species (e.g., Northern Goshawk [*Accipiter gentilis*]), a number of quadrangles where breeding was detected fell outside of the potential habitat identified (Fig. 5d).

Potential habitat models for eight species showed a significant or nearly significant ($p < 0.10$) correlation between the model and the number of detections recorded by point count in each LTA (Table 2). In general, the models for forest species that do not rely on edge performed best, especially Black-throated Blue Warbler (*Dendroica caerulescens*), Canada Warbler, Least Flycatcher, and Wood Thrush (*Hylocichla mustelina*) with correlation coefficients >0.4.
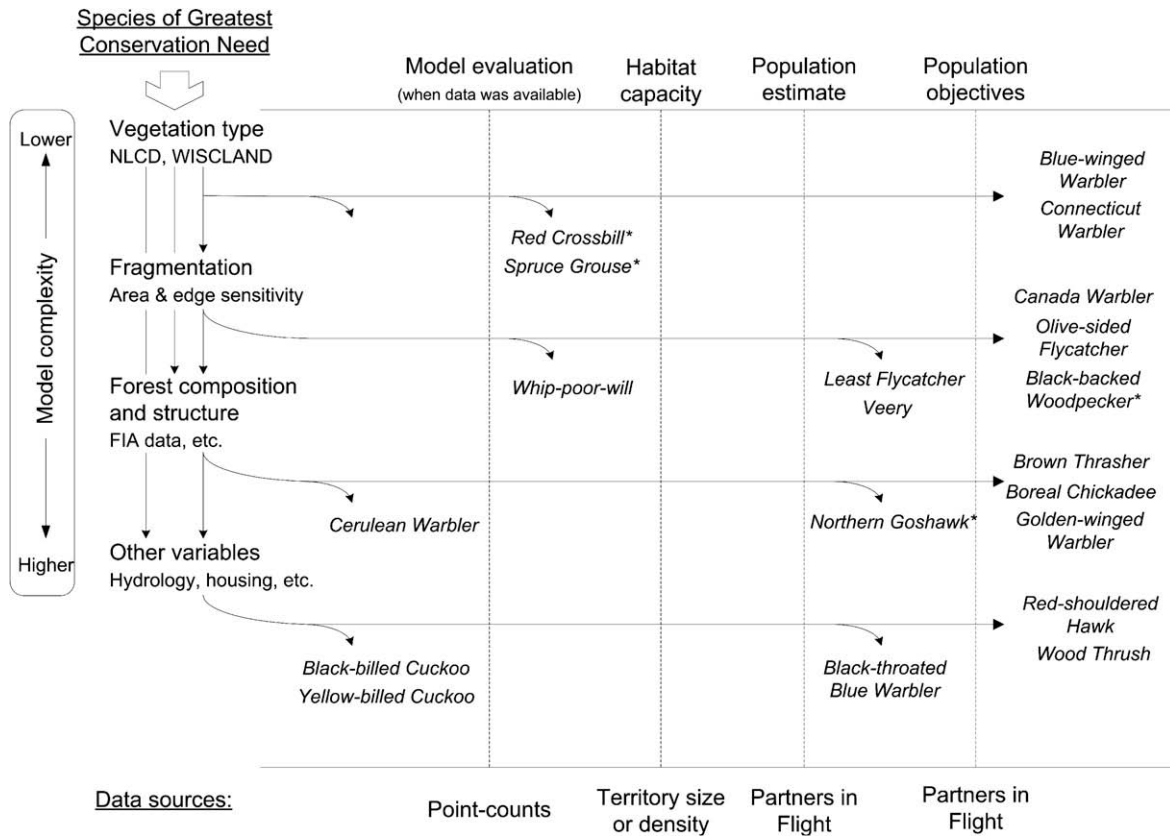
Fig. 4. Flowchart representing the degrees of specificity and endpoints achieved for northern Wisconsin forest avian SGCN potential habitat models. Varying model structure and data availability lead to a range of model complexity and applications. For example, red crossbill falls off when habitat capacity cannot be estimated because of the lack of territory size or density data. Models not supported by independently acquired data fall off at the model valuation step. Those for which insufficient evaluation data were available were carried through the process but are marked with an asterisk.

The evaluation of some non-significant models was limited by low sample sizes (<50 locations, e.g., Red-shouldered Hawk [*Buteo lineatus*], Blue-winged Warbler). For Black-backed Woodpecker (*Picoides arcticus*), Red Crossbill, and Spruce Grouse (*Falcipennis canadensis*), insufficient empirical data were available to conduct a meaningful correlation analysis. Generally, detections were recorded in all LTAs where models had predicted potential habitat (Omission error = 0), with the exceptions of the models for Black-throated Blue Warbler, Boreal Chickadee, and Northern Goshawk (*Accipiter gentilis*; Tables 2 and 3).

We estimated habitat capacity for the 13 species for which we had density or territory size estimates (Fig. 6). The PIF population estimates adjusted for the study area were as much as several orders of magnitude smaller than the capacity of the potential habitat, which was expected because intrinsic elements are likely lacking in much of the mapped potential habitat. For eight species, the PIF estimate was close to or below the capacity when intrinsic elements were maintained in 10% of the mapped potential habitat (Fig. 6). However, in the case of the Northern Goshawk, the PIF estimate was close to the potential habitat under 100% occupancy, and the Brown Thrasher PIF estimate corresponded to 64% occupancy of the potential habitat model (Fig. 6).

4. Discussion

Potential habitat models constitute a foundation for conservation planning for all avian SGCN in northern Wisconsin, not just those species for which there are enough data available to build more complex models. Potential habitat models allow a spatially-explicit evaluation of the current habitat conditions over a large spatial extent, with direct implications for conservation efforts. Our models did not attempt to represent the current distribution of a species, but rather determined where the conditions exist for that species' habitat to be present. A portion of the delineated area of potential habitat will be occupied by a species if intrinsic elements are present in the appropriate quantity and configuration (e.g., large trees, landscape context). Models based on the distribution of habitat instead of occupancy are not handicapped by variations in population size, local extinctions and recolonizations due to metapopulation dynamics, or unknown detection rates common in survey data (Early et al., 2008). Habitat distribution models, such as the potential habitat models shown here, thus have the ability to generalize over a large spatial extent (Early et al., 2008), even at coarse resolution (Eyre et al., 2004).

Among bird habitat models based on the literature and expert opinion, those for species dependent on mid-aged to mature deciduous forests tend to perform best (Dettmers et al., 2002), and we found this was also true for northern Wisconsin species. Our models for species associated with young forests, edges, or highly specialized habitat performed unevenly. Early successional or young forests are transient in time and difficult to detect with classified remote sensing data, affecting our ability to model Golden-winged Warbler and Veery, for example. For edge-associated species, such as Brown Thrasher, edge habitat can be more easily inferred as present between contrasting land cover types, but little is known about the species' response to composition, structure, and width of edges, potentially contributing to the weak performance of these species' models. Additionally, the habitat needs of edge-associated species such as Yellow-billed and Black-billed Cuckoos are little
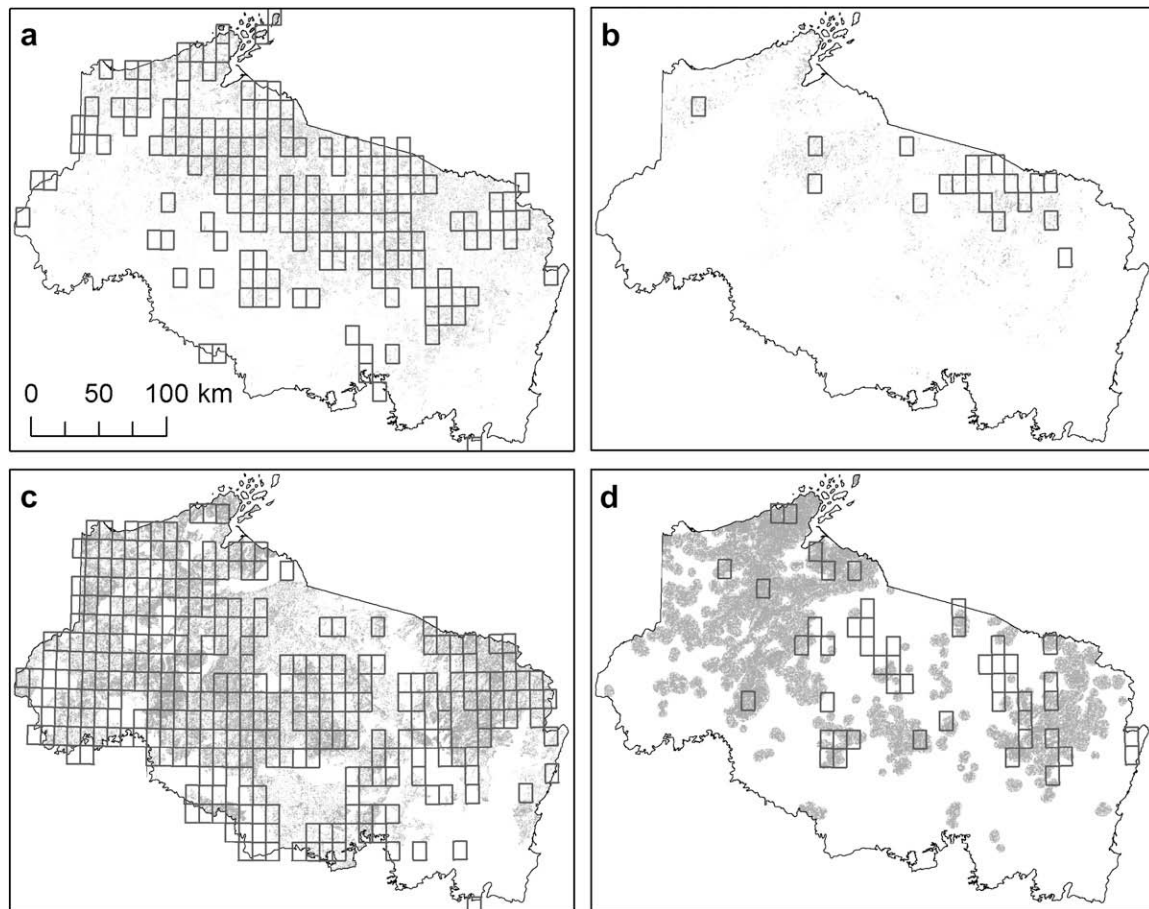
Fig. 5. Potential habitat models for (a) Canada Warbler, (b) Boreal Chickadee, (c) Golden-winged Warbler, and (d) Northern Goshawk. The rectangles represent breeding areas.

Table 2
Potential habitat model comparisons with empirical data. Spearman rank r values provide a measure of the strength of the correlation between the relative amount of potential habitat by LTA and the number of detections recorded. The omission error rate is 1 – (the number of occupied LTAs for which no potential habitat was predicted/the number of occupied LTAs).

	No. of detections	No. of locations detected	No. of locations surveyed	Spearman rank correlation r	p[a]	No. of occupied LTAs	Omission rate at the LTA level[b]
Black-billed Cuckoo	237	221	1957	−0.209		27	0.00
Black-throated Blue Warbler	261	202	1957	0.730	***	17	0.12
Blue-winged Warbler	46	39	1957	0.429		15	0.00
Boreal Chickadee	82	13	1957	0.739	*	7	0.43
Brown Thrasher	369	253	1957	0.540	**	18	0.00
Canada Warbler	449	374	1957	0.415	**	29	0.00
Cerulean Warbler	80	33	1957	-0.138		17	0.00
Connecticut Warbler	118	77	1957	0.454	**	27	0.00
Golden-winged Warbler	505	412	1957	0.247		26	0.00
Least Flycatcher	2938	1558	1957	0.709	***	35	0.00
Northern Goshawk	100	39	39[c]	0.098		41	0.07
Olive-sided Flycatcher	138	117	1957	0.244		16	0.00
Red-shouldered Hawk	94	35	722	0.092		12	0.00
Veery	2275	1672	1957	0.255		35	0.00
Whip-poor-will	148	42	125	0.497	*	5	0.00
Wood Thrush	620	472	1957	0.533	***	25	0.00
Yellow-billed Cuckoo	117	105	1957	−0.334		23	0.00
Black-backed Woodpecker	28	13	1957	na[d]		13	0.00
Red Crossbill	7	7	1957	na		4	0.00
Spruce Grouse	22	22	22[c]	na		9	0.00

[a] Key: *: 0.10 > p > 0.05; **: 0.05 > p > 0.01; ***: 0.01 > p.
[b] Proportion of LTAs with detections that also contain potential habitat.
[c] These values correspond to the number of sites were these species were opportunistically observed, as opposed to systematically surveyed.
[d] Correlations were not conducted for species with <30 detections.

known, and recent work suggests that at least for the latter, habitat associations may be complicated by area-sensitivity (Thogmartin

and Knutson, 2007). Lastly, models built at large spatial scales may perform poorly for species that specialize on habitats that

Table 3
Population estimates and objectives from Partners in Flight (PIF), and corresponding habitat objectives for twenty avian forest species of concern for northern Wisconsin.

Species	Population estimate	Global PIF population objectives[a]	Percentage of global population in WI	Regional PIF risk score[b]	Population target[c]	Minimum habitat needed (ha)[d]	Percentage of potential habitat
Black-backed Woodpecker	200	Maintain	<0.1	15	200	3000	1.5%
Black-billed Cuckoo	38 176	n.a.	5.3	16	38 176	Unknown[e]	n.a.[f]
Black-throated Blue Warbler	9000	n.a.	0.5	17	9000	28 125	6.3%
Blue-winged Warbler	2441	50% increase	3.2	14	3661	46 940	1.6%
Boreal Chickadee	900	Maintain	<0.1	11	900	11 250	4.2%
Brown Thrasher	53 978	Maintain	2.1	14	53 978	94 462	63.7%
Canada Warbler	17 588	50% increase	1.3	17	26 383	13 191	2.3%
Cerulean Warbler	1733	100% increase	0.5	15	3466	4030	n.a.[f]
Connecticut Warbler	9430	Maintain	0.9	17	9430	1697	0.5%
Golden-winged Warbler	41 939	100% increase	22.4	19	83 877	23 066	0.8%
Least Flycatcher	166 494	n.a.	1.4	14	166 494	55 498	2.3%
Northern Goshawk	1500	n.a.	0.3	14	1500	1 944 750	100%
Olive-sided Flycatcher	855	100% increase	0.1	14	1710	8552	3.3%
Red Crossbill	9924	n.a.	0.1	10	9924	Unknown[e]	n.a.
Red-shouldered Hawk	1071	Maintain	0.2	10	1071	114 911	13.5%
Spruce Grouse	n.a.	Maintain	n.a.	12	n.a.	Unknown[e]	n.a.
Veery	305 690	n.a.	2.6	16	305 690	311 928	17.9%
Whip-poor-will	23 669	n.a.	1.7	15	23 669	Unknown[e]	n.a.
Wood Thrush	92 389	50% increase	1.2	14	138 584	301 270	n.a.[e]
Yellow-billed Cuckoo	5789	n.a.	0.2	12	5789	5462	n.a.[f]

[a] In the absence of PIF objective, the minimum habitat value was based on an objective of maintaining the current population.
[b] For boreal hardwood transition region. A high score denotes high endangerment.
[c] Based on global PIF objective.
[d] To meet population target. Based on territory size or density; see Section 2.
[e] No reliable territory size or density estimate available.
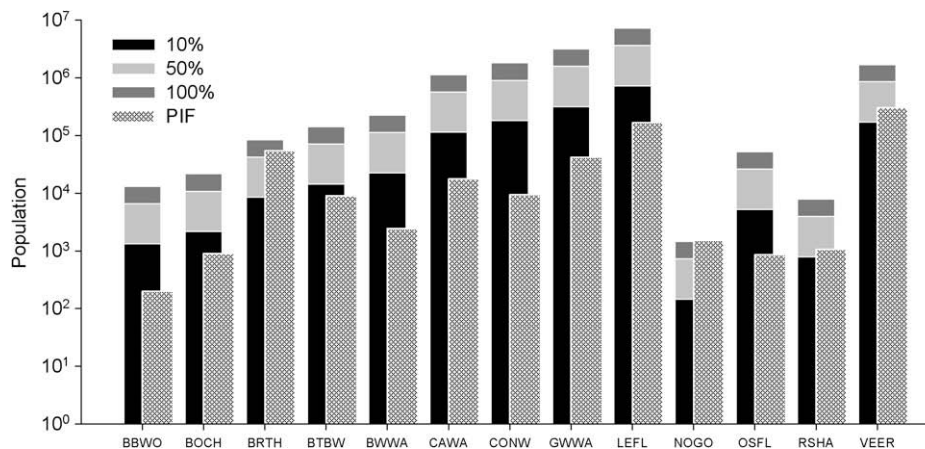[f] Model not supported by the evaluation analysis.

Fig. 6. Population estimates derived from Partners in Flights models for forest bird species of greatest conservation concern in northern Wisconsin, compared to potential habitat models with intrinsic elements present on 10%, 50%, and 100% of mapped potential habitat. Note the logarithmic scale on the y axis. No evaluation data were available for the Black-backed Woodpecker model. Species codes are: BBWO: Black-backed Woodpecker, BOCH: Boreal Chickadee, BRTH: Brown Thrasher, BTBW: Black-throated Blue Warbler, BBWA: Blue-winged Warbler, CAWA: Canada Warbler, CONW: Connecticut Warbler, LEFL: Least Flycatcher, NOGO: Northern Goshawk, OSFL: Olive-sided Flycatcher, RSHA: Red-shouldered Hawk, VEER: Veery, WOTH: Wood Thrush.

occur very locally (Meggs et al., 2004), although our model did perform well for Connecticut Warbler's habitat, which in Wisconsin consists of shrubby margins of coniferous swamps (Robbins, 1991), an inherently localized habitat.

We used independent empirical data to evaluate our models, and the best supported ones (Black-throated Blue Warbler, Brown Thrasher, Canada Warbler, Connecticut Warbler, Least Flycatcher, and Wood Thrush) had a statistically significant correlation with the number of detections at point counts. The models for Boreal Chickadee and Whip-poor-will had low but not significant p values ($0.10 > p > 0.05$) with a large r value (0.739 and 0.497, respectively). Low sample size may have reduced the statistical significance of these models since both of these species were detected at few sites. Most models were conservative, with 17 showing no omission errors at the LTA level. High omission error rates were

found for Black-throated Blue Warbler and Boreal Chickadee; this is due to exclusion from consideration as potential habitat of entire LTAs that did not meet a threshold value for an important variable (winter deer density and black spruce and balsam fir density, respectively). Commission error rates were not calculated as the models represent potential habitat, which does not imply occupation of the species throughout the area.

Data on the distribution of intrinsic elements over large areas are not usually available. However, land managers often have information at finer spatial scales about these critical elements of a species' habitat (e.g., at the scale of a county, state, or national forest). For example, logging history known by a property manager can be used to identify early successional forests, an intrinsic habitat element important for some species. This field-level knowledge of both an area's current conditions and its potential for

sustaining a species can be used to estimate the probability that a mapped area of potential habitat is in fact occupied habitat, or to facilitate planning efficient management actions for increasing habitat suitability. The identification of intrinsic elements can provide explicit guidance toward meeting conservation goals. Thus, managers can enhance critical elements of forest structure or composition to increase the proportion of potential habitat that can host the species. Several of the intrinsic elements identified, such as early successional stage or the presence of snags, can be promoted through common forestry operations.

Unlike inductive habitat models relying on correlates between habitat variables and animal occupancy or abundance, our model structure accommodates distributions that vary due to environmental conditions or metapopulation dynamics (O'Connor, 2002; Early et al., 2008). Potential habitat models integrate knowledge acquired over larger spatial extents and longer periods of time than traditional habitat models. As such, potential habitat models are akin to GAP analysis models, which integrate occurrence data, habitat associations, and expert opinion to create broad scale maps of predicted distributions (Scott et al., 1993). However, the potential habitat models proposed here are not dependent on the availability of large amounts of occurrence data, making them more useful for species for which only limited data is available.

There are parallels between our approach and hierarchical habitat selection (Johnson, 1980), but there are differences as well. The nested elements that were used were largely determined by the availability of data at broad spatial scales; were it possible to map intrinsic elements such as density of snags at the regional scale, we would. With evolving protocols in FIA data collection, this may be possible in the future. While it is true that intrinsic elements are usually features that occur spatially and temporally at scales smaller than the habitat constraints, they also include broader scale features that are simply not currently adequately observed at the regional scale (e.g., forest age, fallow/abandoned fields). On the other hand there are indeed parallels between the spatial scales over which we identify potential habitat and those spanning landscapes analyses (O'Neill et al., 1989).

The use of classified remote sensing data introduced a certain level of uncertainty. For the NLCD data, accuracy assessments for forest (93–99%) categories are high, but accuracies were lower for scrub-shrub and forested wetland categories (75–82%). Fragmentation, patch size and distance-based habitat constraints were affected by this uncertainty and can propagate classification errors. Because of this, interpretation of the results for small areas needs to be done with care, but bias is less likely at the LTA-scale.

Temporal considerations also need to be understood. Potential habitat models reflect habitat conditions at the time of acquisition of the predictive data. When using potential habitat models, just as when using any models, managers need to determine the extent and nature of changes that could have occurred since data acquisition, and decide whether these changes would affect the model's usefulness. However, the data used at the habitat group level (NLCD) are relatively temporally stable due to their coarse classification. Habitat constraints can be sensitive to change: for example, a new road will increase edge and decrease patch size. Intrinsic elements will tend to be the most dynamic, because interventions such as logging will reduce a stand's age, and change the availability of large trees or snags.

For most species, the estimated amount of habitat needed to meet PIF-based population targets appears to be <10% of the mapped potential habitat; in other words, a relatively small proportion of all potential habitat in northern Wisconsin needs to contain the intrinsic elements in order to be considered suitable habitat for a given species. However, for any species the spatial arrangement of habitat is crucial to population viability: connectivity needs to be maintained by considering dispersal distance,

habitat patch arrangement, and matrix composition. Concerns about connectivity extend beyond the state's boundaries, especially for the species occurring at the northern (Cerulean Warbler [*Dendroica cerulea*]) or southern (e.g., Boreal Chickadee, Olive-sided Flycatcher [*Contopus cooperi*]) edge of their range. These species may rely on dispersal from areas closer to the center of their range to support viable populations. Connectivity is particularly crucial for maintaining Wisconsin populations of boreal species, because these birds are likely to be disproportionally affected by climate change as their range contracts northward (Virkkala et al., 2008). Interestingly, habitat capacity and the PIF estimate were nearly identical for Northern Goshawk, suggesting that all remaining habitat for Northern Goshawk in Wisconsin needs to be kept in suitable condition in order to meet PIF conservation objectives for the species. For this species a broader perspective analysis (e.g., the Bird Conservation Region scale) would be useful for understanding patterns of habitat use and suitability.

Our study also revealed a surprisingly large number of species for which basic natural history data are missing, even though North American birds are among the most studied taxa. The analysis of potential habitat was carried to various stages of specificity (Fig 4), highlighting the paucity of data on habitat selection, occurrence, and territory size or density for many species (e.g. Spruce Grouse, Whip-poor-will, Fig. 4). These gaps support the assertion that descriptive research remains necessary for ecological modeling (Haila and Margules, 1996; O'Connor, 2002). Field research efforts should be designed in concert with modelers to identify habitat associations that can be used to quantify habitat on large spatial scales. Variables like soil type (which can be correlated with fine scale habitat features), topography (which can be mapped at increasingly fine resolution with today's remote sensing tools), and other indirect habitat attributes might be the most useful products of local habitat studies for broad scale conservation efforts.

When faced with the need to manage species of conservation concern in a working landscape, a "good" model is one that leads to better decisions than could be made without it (Milspaugh et al., 2009). For many species, there are no detailed presence data available to build statistical survey-based models, resulting in a dearth of broad-scale information available to managers. The value of the approach described here is that it allows refinement of broad scale models through to integration of data collected at multiple scales, and may easily be customized. Potential habitat models provide guidance to managers, highlighting which intrinsic habitat elements should be managed for, and identifying research priorities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.04.025.

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